



First fossil occurrence of a filefish (Tetraodontiformes; Monacanthidae) in Asia, from the Middle Miocene in Nagano Prefecture, central Japan

YUSUKE MIYAJIMA¹, FUMIO OHE², HAKUICHI KOIKE³ & HIROSHIGE MATSUOKA¹

¹Department of Geology and Mineralogy, Kyoto University, Sakyo-ku, Kyoto 606-8502, Japan.

E-mail: yusukemiya@kueps.kyoto-u.ac.jp

²5-77, Harayamadai, Seto City, Aichi 489-0888, Japan

³Shinshushinmachi Fossil Museum, 88-3, Kamijo, Shinshushinmachi, Nagano City, Nagano, 381-2404, Japan

Abstract

A new fossil filefish, *Aluterus shigensis* **sp. nov.**, with a close resemblance to the extant *Aluterus scriptus* (Osbeck), is described from the Middle Miocene Bessho Formation in Nagano Prefecture, central Japan. It is characterized by: 21 total vertebrae; very slender and long first dorsal spine with tiny anterior barbs; thin and lancet-shaped basal pterygiophore of the spiny dorsal fin, with its ventral margin separated from the skull; proximal tip of moderately slender first pterygiophore of the soft dorsal fin not reaching far ventrally; soft dorsal-fin base longer than anal-fin base; caudal peduncle having nearly equal depth and length; and tiny, fine scales with slender, straight spinules. The occurrence of this fossil filefish from the Bessho Formation is consistent with the influence of warm water currents suggested by other fossils, but it is inconsistent with the deep-water sedimentary environment of this Formation. This is the first fossil occurrence of a filefish in Asia; previously described fossil filefishes are known from the Pliocene and Pleistocene of Italy, the Pliocene of Greece, and the Miocene and Pliocene of North America. These fossil records suggest that the genus *Aluterus* had already been derived and was widely distributed during the Middle Miocene with taxa closely resembling Recent species.

Key words: *Aluterus*, Bessho Formation, filefish, Japan, Middle Miocene, new species

Introduction

Recent filefishes of the family Monacanthidae are widely distributed in tropic and temperate shallow waters of the Atlantic, Indian, and Pacific oceans (e. g., Hutchins, 1977; Nakabo, 2000; Matsuura, 2002; Nelson, 2006). The family consists of about 32 genera and about 102 species (Nelson, 2006), being one of the most speciose families of the order Tetraodontiformes (Sorbini and Tyler, 2004). However, fossil filefishes have been known only from the Pliocene and Pleistocene of Italy (Landini and Menesini, 1978; Sorbini, 1988; Landini and Sorbini, 1992; Landini and Sorbini, 1993; Sorbini and Tyler, 2004), the Pliocene of Greece (Gaudant, 2001), and the Miocene and Pliocene of North America (Purdy *et al.*, 2001).

A fossil filefish was discovered by the first author from the Miocene Bessho Formation, Nagano Prefecture, central Japan on 9 September 2012. This is the first fossil occurrence of a filefish in Asia. Although this fossil specimen lacks the skull and pelvic girdle, it clearly belongs to the genus *Aluterus* and has a unique set of characters which very closely resembles those of the extant *Aluterus scriptus* (Osbeck, 1765), but the fossil also differs from all of the extant species of the genus and it is described herein as a new fossil species of that genus.

Geological setting

The fossil filefish reported herein was discovered in an outcrop of the Tazawa black mudstone Member (Tanaka and Seki, 1966) of the Bessho Formation (Honma, 1927) in the riverbed (36°19'37"N, 137°59'40"E) of the Hofukuji River at Sorimachi, Matsumoto City, Nagano Prefecture, central Japan (Figure 1). The Bessho Formation

is mainly composed of black mudstone considered to have been deposited at the deep seabed formed with the opening of the Japan Sea (Harayama, 2006; Kobayashi, 2006). The sea of northern Fossa Magna, where the Bessho Formation was deposited, was connected with the Pacific Ocean at that time (Kano *et al.*, 1991; Kosaka *et al.*, 1992). The Bessho Formation is estimated to be correlated to the N. 9-N. 10 planktonic foraminiferal zone of Blow (1969) in the Middle Miocene (Kosaka *et al.*, 1992). In addition, Kosaka *et al.* (1998) show that the lower part of the Bessho Formation corresponds to the boundary between the N. 8 and N. 9 based on planktonic foraminifers. The Tazawa black mudstone Member intercalates limestones, and recently the age of one of these, the Anazawa Limestone, was estimated at 13.6-13.1 Ma based on the calcareous nannofossil assemblage (Kato *et al.*, 2011). Kato *et al.* (2011) also reported a benthic foraminiferal fossil assemblage living in upper to upper middle bathyal depths from the limestone.

The outcrop which yielded the fossil consists of massive and parallel laminated dark gray siltstone, and the fossil was found at the parallel laminated horizon (Figure 2) lying parallel with the bedding plane. This horizon also yielded abundant fossil fish scales such as of Clupeidae, Myctophidae and Sparidae, and many fossil fish skeletons, including those of Clupeidae, Macrouridae, and cf. *Gasterosteus aculeatus* (Gasterosteidae). In addition, molluscan fossils such as *Delectopecten peckhami* (Pectinidae) and *Mizuhobaris izumoensis* (Argonautidae), and gooseneck barnacles and plants are also found at this horizon. This horizon is characterized by the occurrence of gennoishi (glendonite). A new fossil sperm whale, *Brygmophyseter shigensis*, was discovered from this outcrop in 1986 (Hirota and Barnes, 1995).

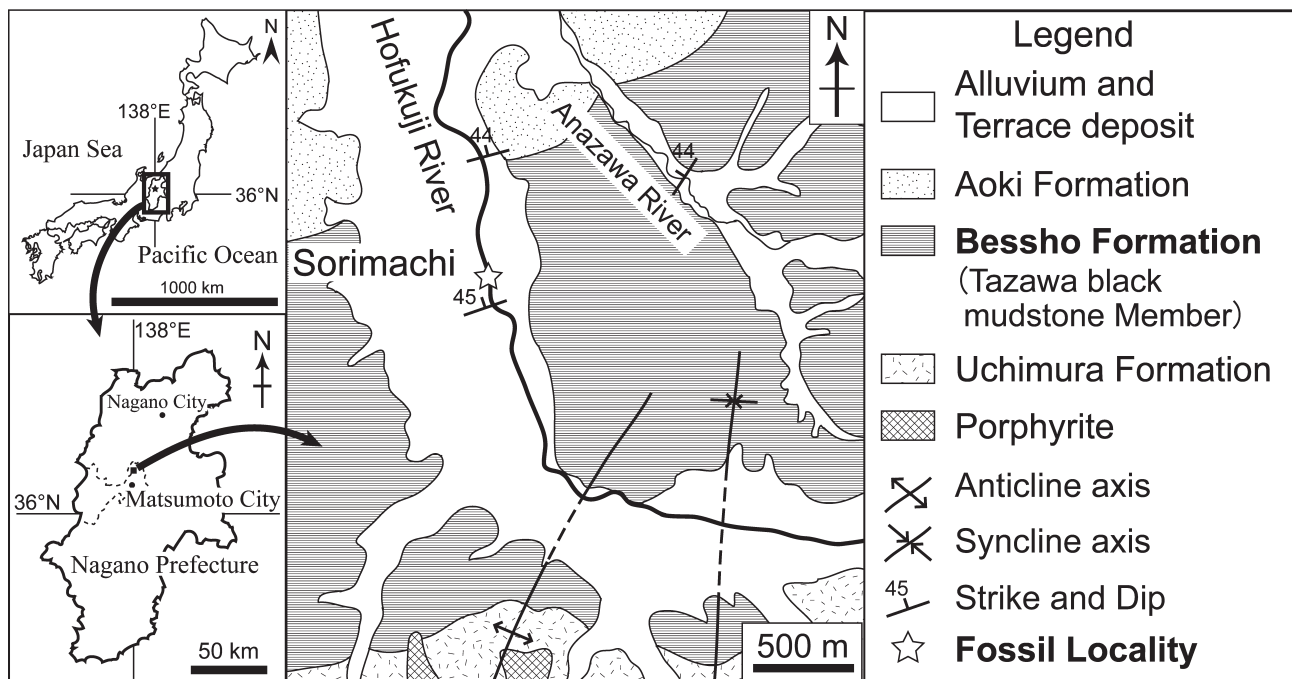


FIGURE 1. Geological map of the Sorimachi area in Matsumoto City and the locality of the fossil filefish. The geological map is modified from Seki (1983).

Material and preparation

The holotype of a new fossil species described herein was finely examined and drawings were prepared using a microscope. Measurements were made to the nearest 0.1 mm using calipers. Scanning electronic microscope (SEM) images of the scales of the holotype of a new fossil filefish and those of the extant *A. scriptus* were taken using TM3000 (HITACHI Co., Ltd., Japan). The scales of the fossil were platinum deposited using Magnetron sputter MSP-1S (Vacuum Device Inc., Japan) before SEM observation. The holotype is deposited in the Matsumoto City Shiga Fossil Museum, 85-1, Nanaarashi, Matsumoto City, Nagano Prefecture, central Japan (MSFM 00606).

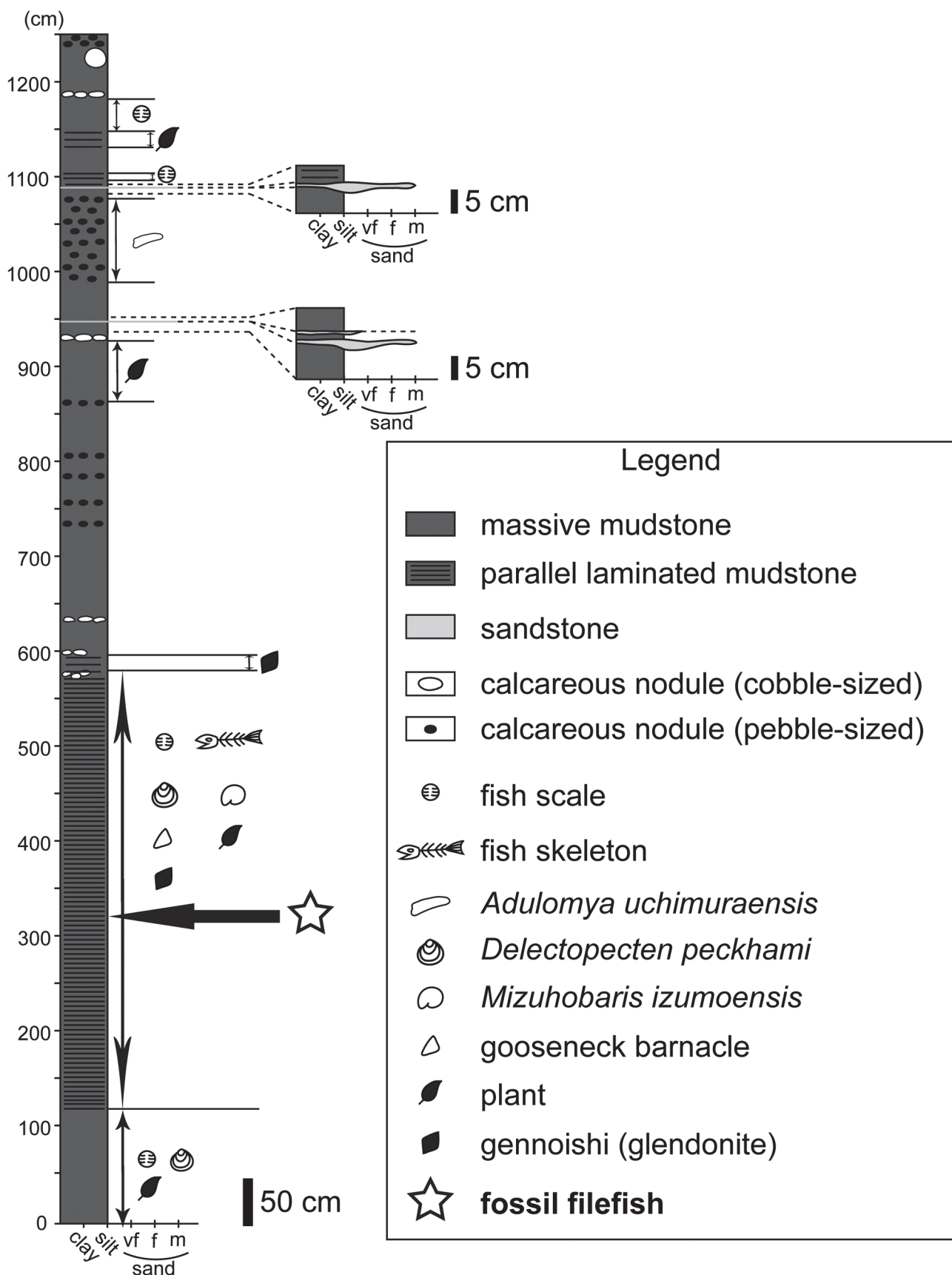


FIGURE 2. The columnar section at the fossil locality in Figure 1 showing the fossil horizon.

Dried skeletal specimens of *Aluterus* species deposited in the Department of Geology and Mineralogy, Kyoto University, Japan (KUGRF) were used for comparison with the new fossil filefish: *Aluterus scriptus*, KUGRF 121201, 202.8 mm in standard length (SL) and KUGRF 121202, 230.3 mm SL, both specimens from Philippines; *Aluterus monoceros*, KUGRF 121101, 371.3 mm SL and KUGRF 121102, 396.3 mm SL, both specimens from the Japan Sea, commercial harbor of Sakai Minato City, Tottori Prefecture, southwestern Japan. Radiographs of alcohol preserved specimens from the extant fish collections of the Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, USA (USNM) were also used for comparison: *Aluterus schoepfii*, USNM 155983, ca. 143 mm SL, Gulf of Mexico, Texas, USA and USNM 204819, standard length unknown, Atlantic, South Carolina, USA; *Aluterus scriptus*, USNM 402324, 460 mm SL, Atlantic, Palm Beach County, Florida, USA, USNM 407016, 90 mm SL, Pacific, Luzon, Cagayan, Philippines and USNM 416202, 285 mm SL, Caribbean Sea, Curlew Bank, Belize; *Aluterus heudelotii*, USNM 405092, ca. 239 mm SL, Atlantic, Cape Verde, USNM 405171, ca. 292 mm SL and USNM 405172, ca. 213 mm SL, both specimens from Atlantic, Boa Vista, Cape Verde. In addition, specimens of *Aluterus scriptus* were examined from the extant fish collections of the Maizuru Fisheries Research Station, Field Science Education and Research Center, Kyoto University, Japan (FAKU): FAKU S60, 240.2+ mm SL, bent specimen, the Japan Sea, Tsushima Island, Nagasaki Prefecture, Japan, FAKU 36509, 234.3 mm SL, FAKU 36510, 196.2 mm SL, FAKU 36511, 185.5 mm SL and FAKU 36512, 237.2 mm SL, all of these from the Japan Sea, off Shimane Prefecture, Japan, FAKU 41193, 320.5 mm SL, the East China Sea, Kayama Island, Ishigaki City, Okinawa Prefecture, Japan, FAKU 101991, 176.3 mm SL, the East China Sea, Ishigaki City, Okinawa Prefecture, Japan, FAKU 103187, 272.7 mm SL and FAKU 103188, 217.9 mm SL, locality of both specimens unknown, and FAKU 132252, 309.4 mm SL, Wakasa Bay, Bakuchi Promontory, Maizuru City, Kyoto Prefecture, Japan.

Soft radiograph of the dried skeletal specimens of the extant *Aluterus scriptus* (KUGRF 121201, 121202) were taken by soft radiograph nondestructive inspection system M-60 (SOFTEX, Co., Ltd., Japan) for comparison with the fossil.

Systematic description

Order Tetraodontiformes Berg, 1940

Family Monacanthidae Nardo, 1842

Genus *Aluterus* Cloquet, 1816

Aluterus shigensis sp. nov.

Figures 3–5B, 6–7B, 9

Holotype. MSFM 00606, part and counterpart, collected by Yusuke Miyajima (Kyoto University, Japan).

Locality and horizon. The riverbed (36°19'37"N, 137°59'40"E) of the Hofukuji River at Sorimachi, Matsumoto City, Nagano Prefecture, central Japan (Figures 1 and 2). The Tazawa black mudstone Member (Tanaka and Seki, 1966) of the Middle Miocene Bessho Formation (Honma, 1927), 13.6–13.1 Ma (Kato *et al.*, 2011).

Etymology. The specific name *shigensis* is derived from the old name of the region where the fossil was found, Shiga-Mura village.

Diagnosis. Total vertebrae, 21 (7AV + 14CV). Very slender and long first dorsal spine with tiny anterior barbs. Thin, lancet-shaped single basal pterygiophore supporting two dorsal spines, with its ventral margin separated from the skull. Moderately slender first basal pterygiophore of the soft dorsal fin having its proximal tip located above the middle length of the neural spine of the fifth abdominal vertebra. Soft dorsal-fin base longer than the anal-fin base. Caudal peduncle having nearly equal depth and length. Tiny, fine scales with slender, straight spinules.

Description of holotype. The fossil specimen lacks the skull bones and pelvic girdle, being represented mostly by an articulated axial skeleton (Figures 3 and 4). All of the vertebrae and their neural and haemal spines are preserved. Two dorsal spines supported by a single basal pterygiophore, which is a diagnostic feature of the

Monacanthidae (Tyler, 1980), are preserved. The basal pterygiophores of the soft dorsal fin and the anal fin (on the counterpart) are partially missing. Most of the soft dorsal-fin rays are missing, but several anal-fin rays are preserved. Considering the numbers and preservation states of the pterygiophores and fin rays, the soft dorsal-fin base is longer than the anal-fin base. The ventral part of the compound terminal centrum (Schultze and Arratia, 2013) and the caudal fin are preserved. Tiny, fine scales with spinules (Tyler, 1980; Sorbini and Tyler, 2004) are preserved.

The length of the skeleton from the anterior end of the second abdominal vertebra to the base of the caudal fin (shown as *l* in Figure 3B) is 124.1 mm. Body depth (BD) is more than 65.0 mm. Measurements of the fossil and of specimens of the extant *Aluterus scriptus* are shown in Table 1.

TABLE 1. Measurements of the fossil, *Aluterus shigensis* sp. nov., holotype (MSFM 00606) and specimens of the extant *A. scriptus* (mm). 1DBP: basal pterygiophore of the spiny dorsal fin. “–” indicates that the value cannot be measured.

Specimen	Standard length (SL)	<i>l</i>	Body depth (BD)	Soft dorsal-fin base length	Anal-fin base length	Caudal peduncle length (CL)
fossil (MSFM 00606)	–	124.1	65.0+	63.8+	60.5	19.0
KUGRF 121201	202.8	118.1	72.1	61.3	63.7	11.9
KUGRF 121202	230.3	138.3	80.0	73.4	75.7	12.4

TABLE 1. (Continued)

Specimen	Caudal peduncle depth (CD)	1DBP depth (BPD)	BD/ <i>l</i>	CD/CL	CD/ <i>l</i>	BPD/ <i>l</i>
fossil (MSFM 00606)	23.3	4.9	0.52+	1.23	0.19	0.039
KUGRF 121201	27.8	5.3	0.61	2.34	0.24	0.045
KUGRF 121202	29.6	5.6	0.58	0.21	0.21	0.040

Total vertebrae including compound terminal centrum (C-H in Figure 3) are 21 (7 AV + 14 CV), and this also distinguishes the fossil from balistids which have almost invariably 18 vertebrae (Matsuura, 1979; Tyler, 1980). Although the first abdominal vertebra is disarticulated and displaced anteriorly, the other 20 vertebrae are well articulated in a straight vertebral column. The neural spines of the first to sixth abdominal vertebrae are thin and expanded, but their outlines are obscure and can scarcely be seen using a microscope. The neural spine of only the first abdominal vertebra is oriented anteriorly. The distal end of the neural spine of the second abdominal vertebra is immediately posteroventral to the basal pterygiophore of the spiny dorsal fin. The distal end of the neural spine of the fourth abdominal vertebra is situated close to that of the fifth abdominal vertebra. The neural spine of the fifth abdominal vertebra is immediately anterior to the first pterygiophore of the soft dorsal fin (2DP1 in Figures 3, 4 and 6A) and it is relatively more slender than the other expanded neural spines. The neural spine of the sixth abdominal vertebra is more expanded and higher than that of the fifth abdominal vertebra. Parapophysis of the seventh abdominal vertebra is wide, short and oriented posteriorly. Ribs are absent. Haemal spines are present from the first to thirteenth caudal vertebra. The haemal spine of the first caudal vertebra contacts the first pterygiophore of the anal fin, although the boundary of these two bones is indistinct (Figure 4). The thirteenth caudal vertebra has a posteriorly expanded haemal spine.

The first dorsal spine is very slender and long; it is about 1 mm in width and its preserved length is 32 mm. Tiny anterior barbs are present; that is, the anterior margin of this spine is finely serrated in an orderly manner and the posterior margin is smooth (Figure 5B). There is an inner cavity running along the central axis of this spine in its cross section (Figure 5A, B). The surface of this spine is characterized by grooves parallel to the long axis of the spine. The second dorsal spine, which is placed just behind the base of the first dorsal spine, is tiny and curved posteriorly with a blunt distal end. This is a diagnostic feature of the Monacanthidae, whereas there are three stronger dorsal spines supported by two basal pterygiophores in the Balistidae (Matsuura, 1979; Tyler, 1980).

The first and second dorsal spines are supported by a single basal pterygiophore (1DBP in Figures 3, 4 and 5A). This bone has a thin, lancet-like shape and its ventral margin is separated from the skull. The posterior part of this bone is partly missing, but its posterior end extends to above the neural spine of the second abdominal vertebra. The depth of this basal pterygiophore (BPD) is 4.9 mm (Table 1).

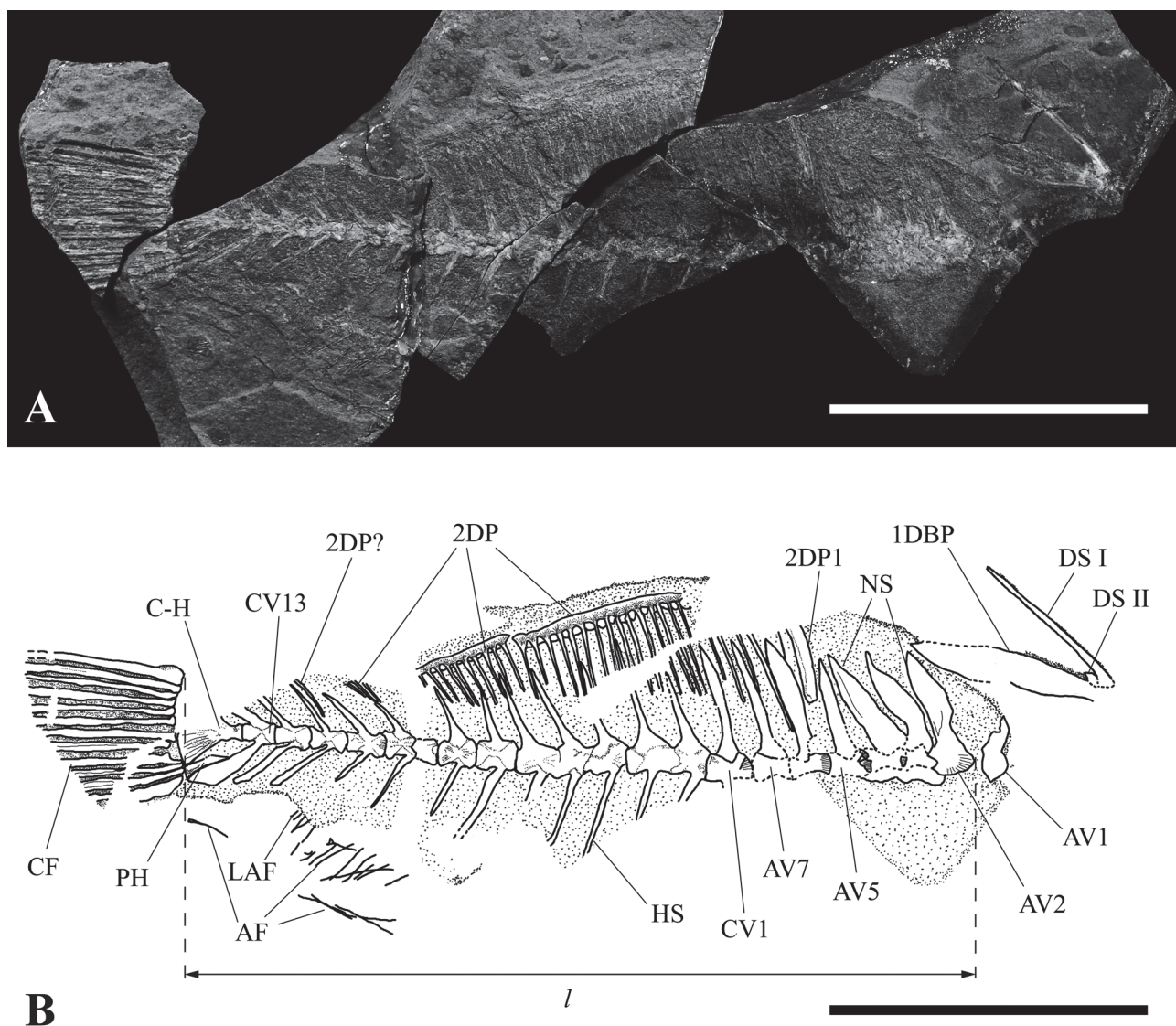


FIGURE 3. *Aluterus shigensis* sp. nov. from the Bessho Formation at Sorimachi, Matsumoto City, Nagano prefecture. Photograph (A) and drawing (B) of the part of the holotype. MSFM 00606. Abbreviations: 1DBP, basal pterygiophore of the spiny dorsal fin; 2DP, pterygiophore of the soft dorsal fin; 2DP1, first pterygiophore of the soft dorsal fin; AF, anal-fin ray; AV1-7, first-seventh abdominal vertebrae; CF, caudal fin; C-H, compound terminal centrum; CV1-13, first-thirteenth caudal vertebrae; DS I, first dorsal spine; DS II, second dorsal spine; HS, haemal spine; LAF, last anal-fin ray; NS, neural spine; PH, parhypural. *l* shows the length of skeleton from second abdominal vertebra to caudal-fin base. Dotted area anterior to caudal fin shows the preservation of scales. Scale bars = 50 mm.

Most parts of the basal pterygiophores of the soft dorsal fin are preserved. There are 34 such basal pterygiophores, and the posterior part of the soft dorsal fin is partly missing. The first and thickest pterygiophore of the soft dorsal fin (2DP1) is moderately slender and its proximal tip, which is located above the middle length of the neural spine of the fifth abdominal vertebra, is blunt (Figure 6A). The second pterygiophore is longer than the other soft dorsal-fin pterygiophores, and its proximal tip is located lower than those of the other pterygiophores and below the middle length of the neural spine of the sixth abdominal vertebra. The pterygiophores are indistinguishably articulated to one another at their distal ends where radial grooves are present on the surfaces, but they are partly broken and displaced slightly dorsally above the second to fifth caudal vertebrae. In monacanthid fishes, most parts of each slender pterygiophore of the soft dorsal and anal fins are connected with one another anteroposteriorly by very thin flanges but such a feature is indistinct in this fossil specimen. The number of pterygiophores between two adjacent neural spines ranges from two to four except for their being a single pterygiophore between the neural spines of the fifth and sixth abdominal vertebrae (Table 2). Only six fin rays of

the soft dorsal fin are preserved at the posterior end of the counterpart, but two of them are disarticulated and displaced (Figures 4 and 6B). The soft dorsal-fin base, from the second to the last pterygiophore of the fin, is longer than the anal-fin base (Table 1). The length of the soft dorsal-fin base of the fossil shown in Table 1 corresponds to the length from the second pterygiophore (2DP2 in Figure 4) to the pterygiophore preserved between the neural spines of the ninth and tenth caudal vertebrae (2DPX in Figure 4), but it seems to be longer because the soft dorsal-fin rays are preserved posteriorly and a slender bone, probably a pterygiophore (2DP? in Figures 3 and 4), is present between the neural spines of the tenth and eleventh caudal vertebrae.

TABLE 2. The numbers of pterygiophores of the soft dorsal fin between adjacent neural spines from that of the fifth abdominal (A5) to that of the thirteenth caudal (C13) vertebrae of the fossil, *Aluterus shigensis* **sp. nov.**, holotype (MSFM 00606) and specimens of the extant *A. scriptus*.

Specimen	Neural spines						
	A5-A6	A6-A7	A7-C1	C1-C2	C2-C3	C3-C4	C4-C5
	Number of pterygiophores of the soft dorsal fin						
fossil (MSFM 00606)	1	2	2	4	3	3	4
KUGRF 121201	1	2	3	3	3	4	4
KUGRF 121202	1	1	3	3	4	4	4
USNM 402324	1	2	3	4	4	4	5
USNM 407016	1	2	3	4	3	4	4
USNM 416202	1	2	3	3	4	4	5

TABLE 2. (Continued)

Specimen	Neural spines							
	C5-C6	C6-C7	C7-C8	C8-C9	C9-C10	C10-C11	C11-C12	C11-C12
	Number of pterygiophores of the soft dorsal fin							
fossil (MSFM 00606)	3	3	4	3?	1	1?	0	0
KUGRF 121201	4	4	5	5	8?	0	0	0
KUGRF 121202	4	4	4	4	7	0	0	0
USNM 402324	4	5	5	6	3	0	0	0
USNM 407016	4	4	5	5	5	0	0	0
USNM 416202	4	4	5	5	5	0	0	0

The pterygiophores of the anal fin are partially preserved on the counterpart (Figure 4); 16 pterygiophores are recognizable at least in part, and the first pterygiophore (AP1 in Figure 4) is thicker than the others. The pterygiophores of the anal fin are absent at least between the haemal spines of the tenth and the last caudal vertebrae. Although there are no pterygiophores preserved between the haemal spines of the ninth and tenth caudal vertebrae, those bones must have been present there because anal-fin rays are present ventrally. There are 21 anal-fin rays preserved, but most of them are disarticulated and displaced.

Although the caudal peduncle is incomplete, the depth and length of it are nearly equal (Table 1), with depth measured vertically from the posterior end of the anal-fin base (the base of the last anal-fin ray, LAF in Figures 3 and 4) to the dorsal margin of the skin of the caudal peduncle, and length measured from the posterior end of the anal-fin base to the ventral edge of the caudal-fin base, following Berry and Vogeley (1961). Although the dorsal part of the caudal skeleton is missing, the triangular compound terminal centrum including an unknown number of vertebral centra and hypurals (Schultze and Arratia, 2013) is preserved. In monacanthid fishes, a horizontal crest for muscle attachment is present at the anterior part of this bone (Matsuura, 1979), but such a feature is poorly preserved and indistinct in this fossil specimen. The parhypural is preserved between the compound terminal centrum and the expanded haemal spine of the thirteenth caudal vertebra, but its shape is indistinct. There are 12 caudal-fin rays.

The scales are very small and fine, and have slender, straight spinules (Figure 7A, B), which are preserved over almost the entire body. Especially along the dorsal margins of the pterygiophores of the spiny and soft dorsal fins, the tiny spinules (one of which is about 0.26 mm in length) of the scales are well preserved.

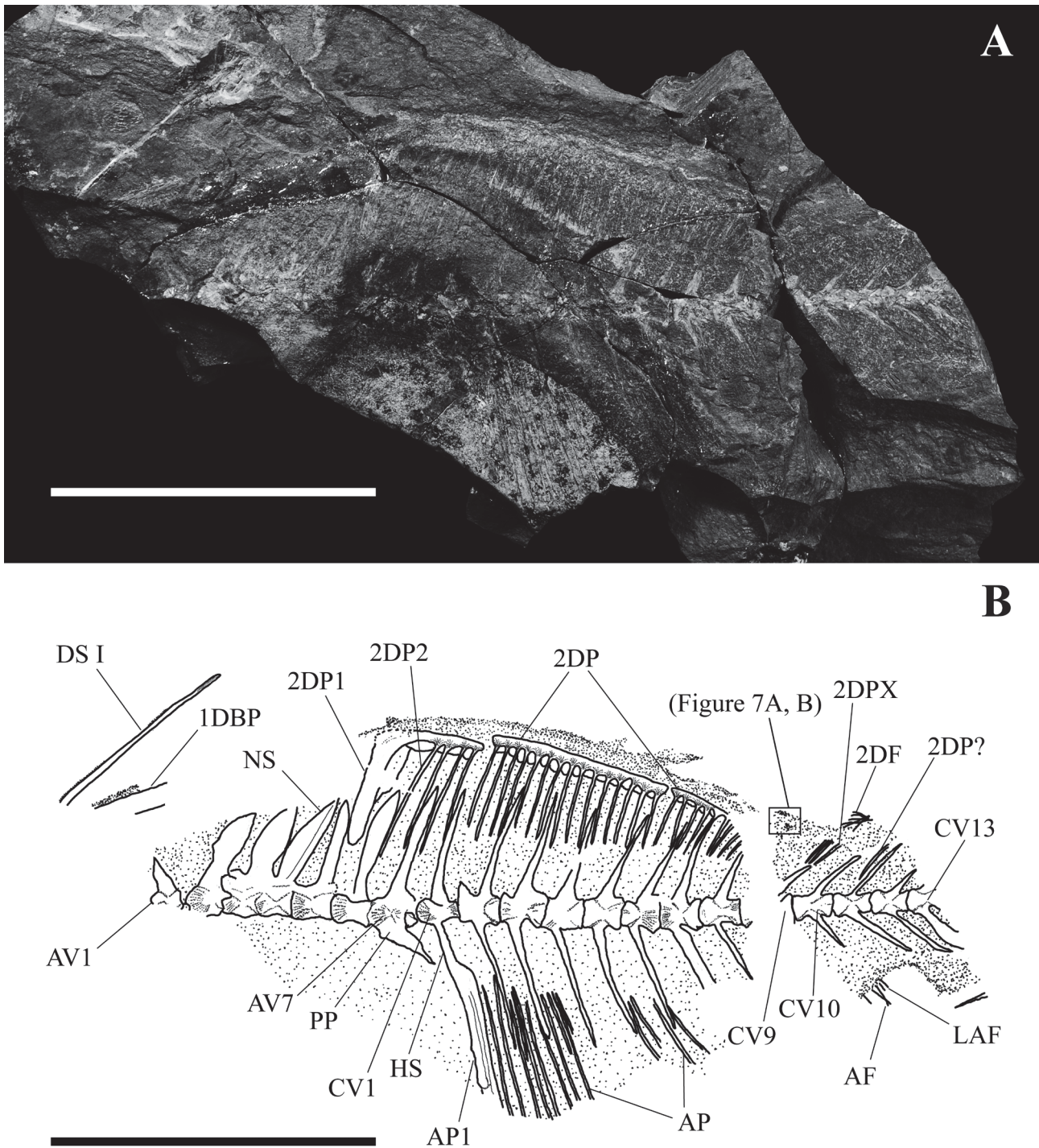


FIGURE 4. *Aluterus shigensis* sp. nov. Photograph (A) and drawing (B) of the counterpart of the holotype. MSFM 00606. Abbreviations: 2DF, soft dorsal-fin ray; 2DP2, second pterygiophore of the soft dorsal fin; 2DPX, pterygiophore of the soft dorsal fin between neural spines of the ninth and tenth caudal vertebrae; AP, pterygiophore of anal fin; AP1, first pterygiophore of anal fin; PP, parapophysis. Other abbreviations as in Figure 3. Dotted area shows the preservation of scales. Square shows the area observed using SEM in Figures 7A and 7B. Scale bars = 50 mm.

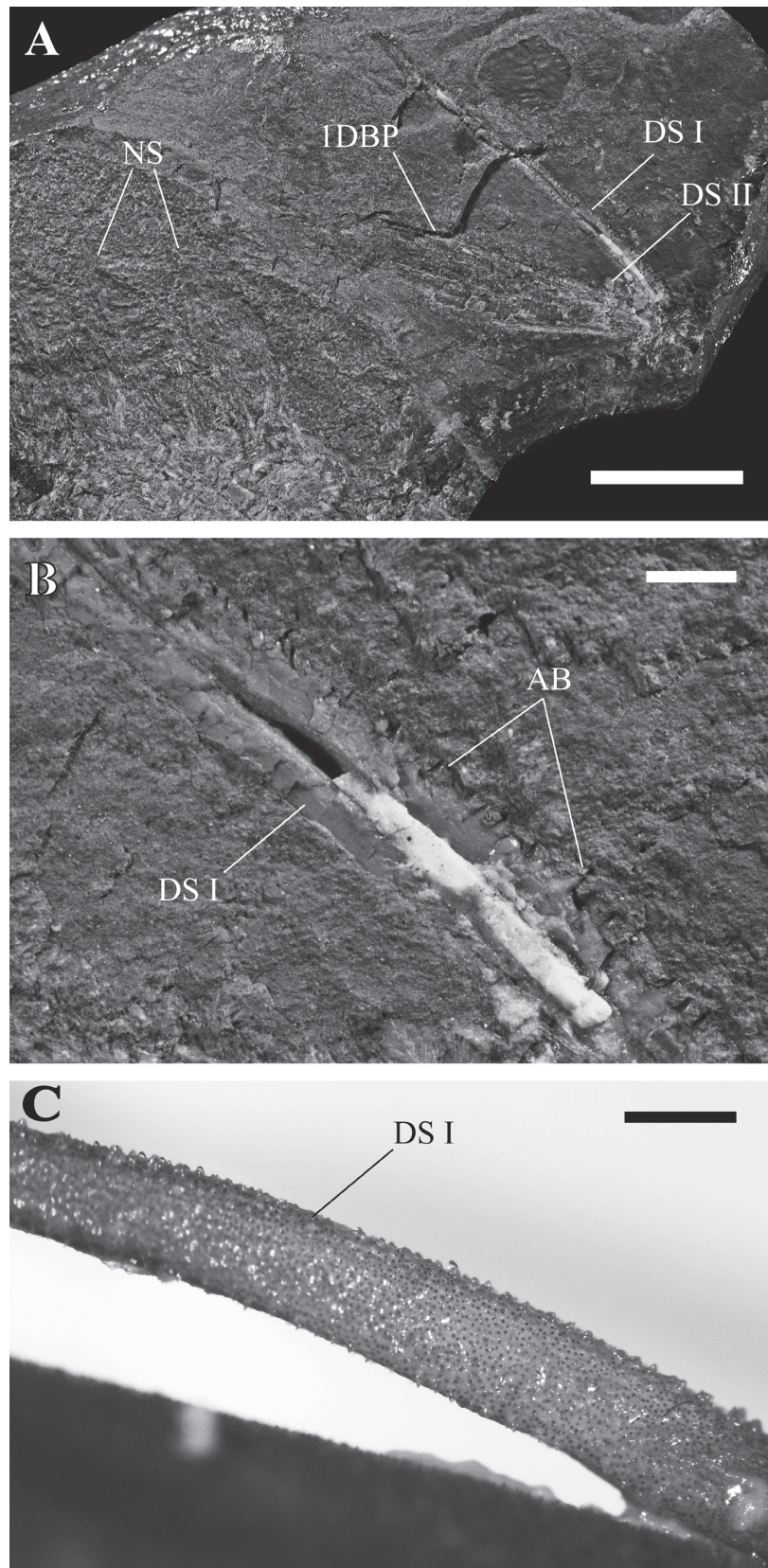


FIGURE 5. Enlarged photographs of the spiny dorsal fin region of the fossil, *Aluterus shigensis* sp. nov., holotype, MSFM 00606 (A and B) and the extant *Aluterus scriptus*, FAKU 36510 (C). **A–B**, *Aluterus shigensis* sp. nov. The spiny dorsal fin region (A) and the first dorsal spine (B) based on the part of the holotype (MSFM 00606); **C**, The spiny dorsal fin of the extant *A. scriptus* (FAKU 36510). Abbreviation AB indicates anterior barbs. Other abbreviations as in Figure 3. Scale bars = 10 mm (A), 1 mm (B and C).

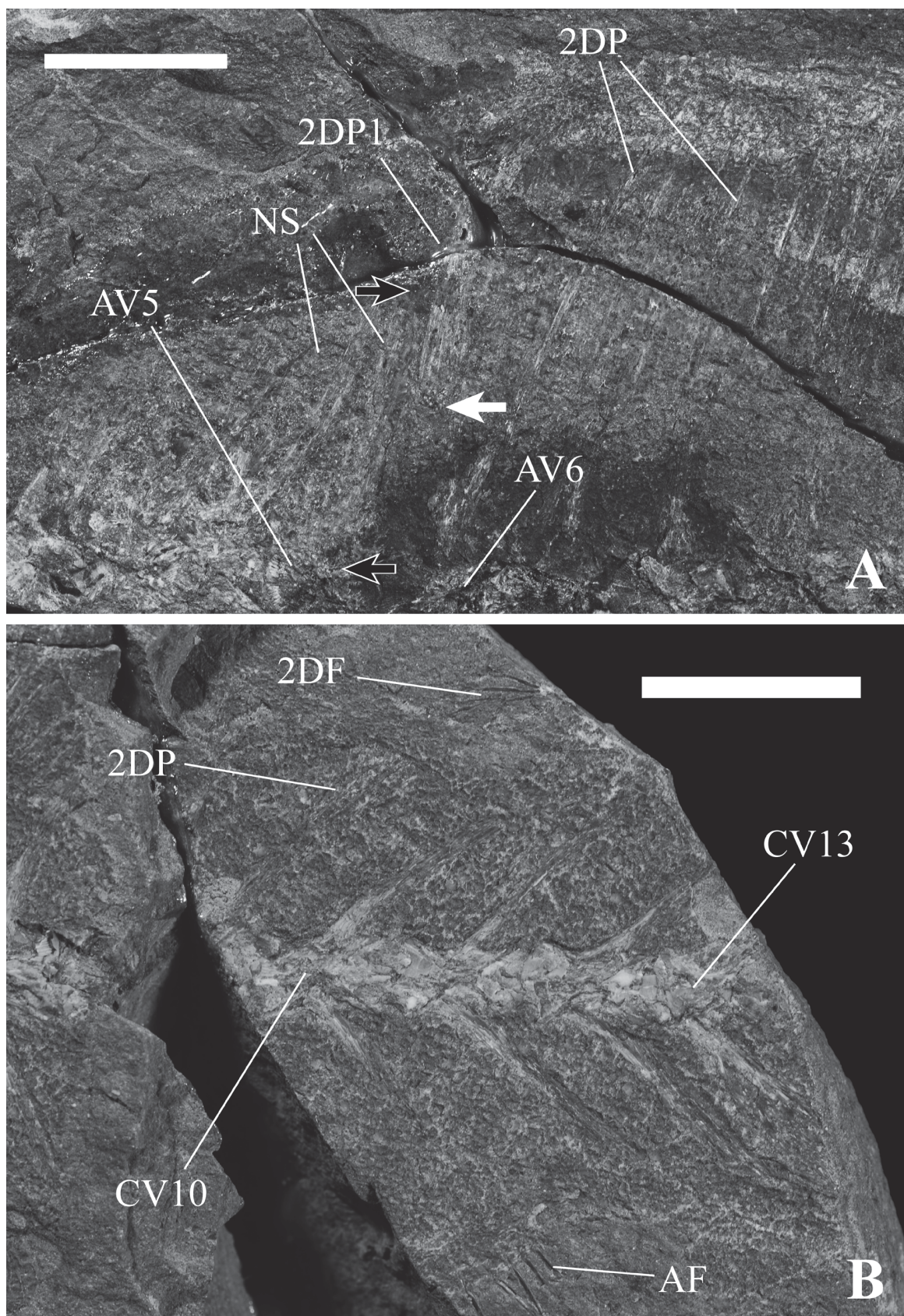


FIGURE 6. *Aluterus shigensis* sp. nov. Enlarged photographs of the anterior region of the soft dorsal fin (A) and the caudal peduncle (B) based on the counterpart of holotype, MSFM00606. Abbreviations as in Figures 3 and 4. White arrow in (A) shows the proximal tip of the first pterygiophore of the soft dorsal fin (2DP1). Black arrows in (A) show the distal end and the base of the neural spine of the fifth abdominal vertebra. Scale bars = 10 mm.

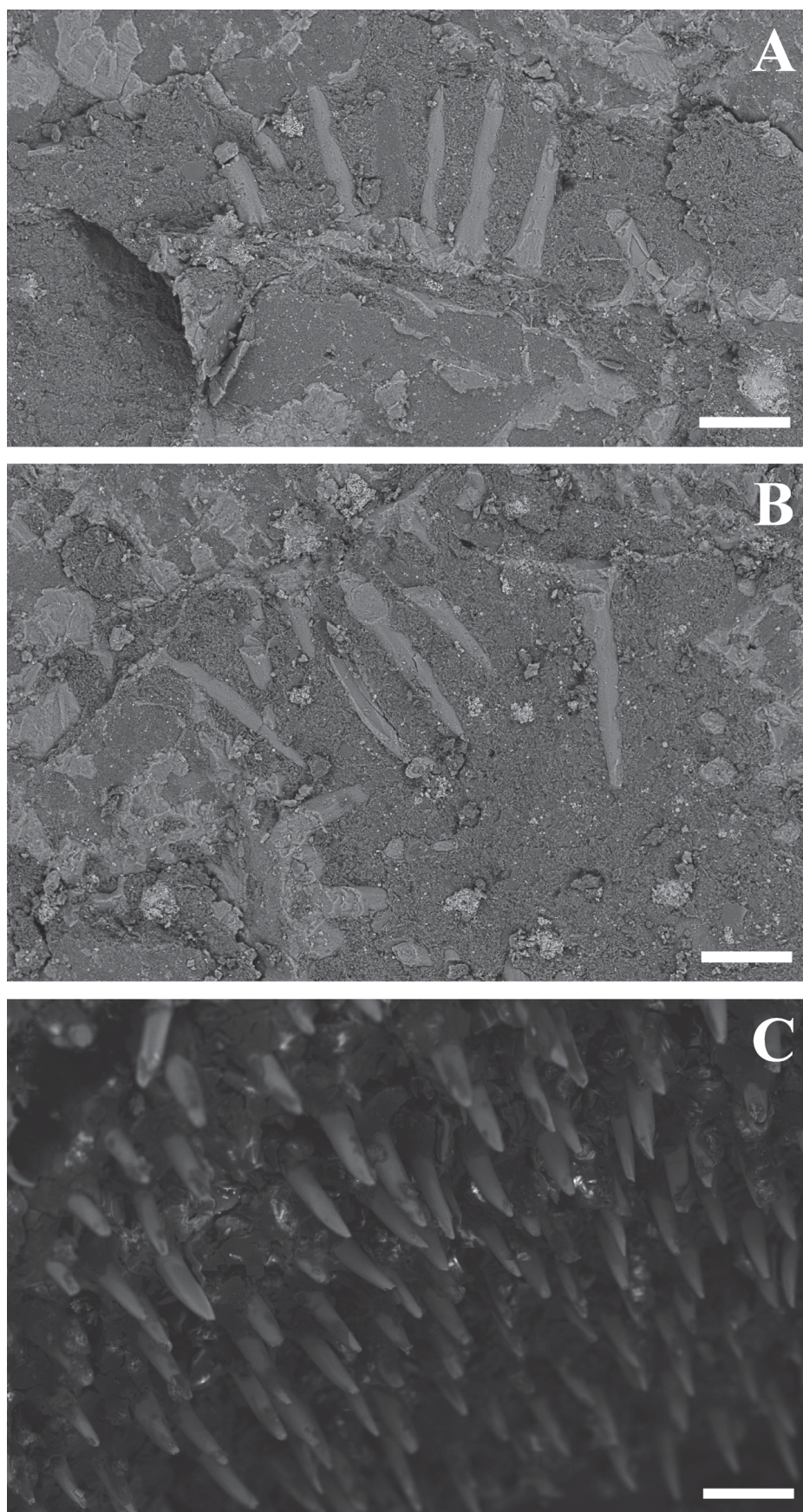


FIGURE 7. Scanning electronic microscope (SEM) images of scales of the fossil, *Aluterus shigensis* **sp. nov.**, holotype, MSFM 00606 (A and B) and *Aluterus scriptus*, KUGRF 121202 (C). Note the close resemblance of the shape and size of scales of the fossil to those of extant *Aluterus* species. Scale bars = 100 μ m.

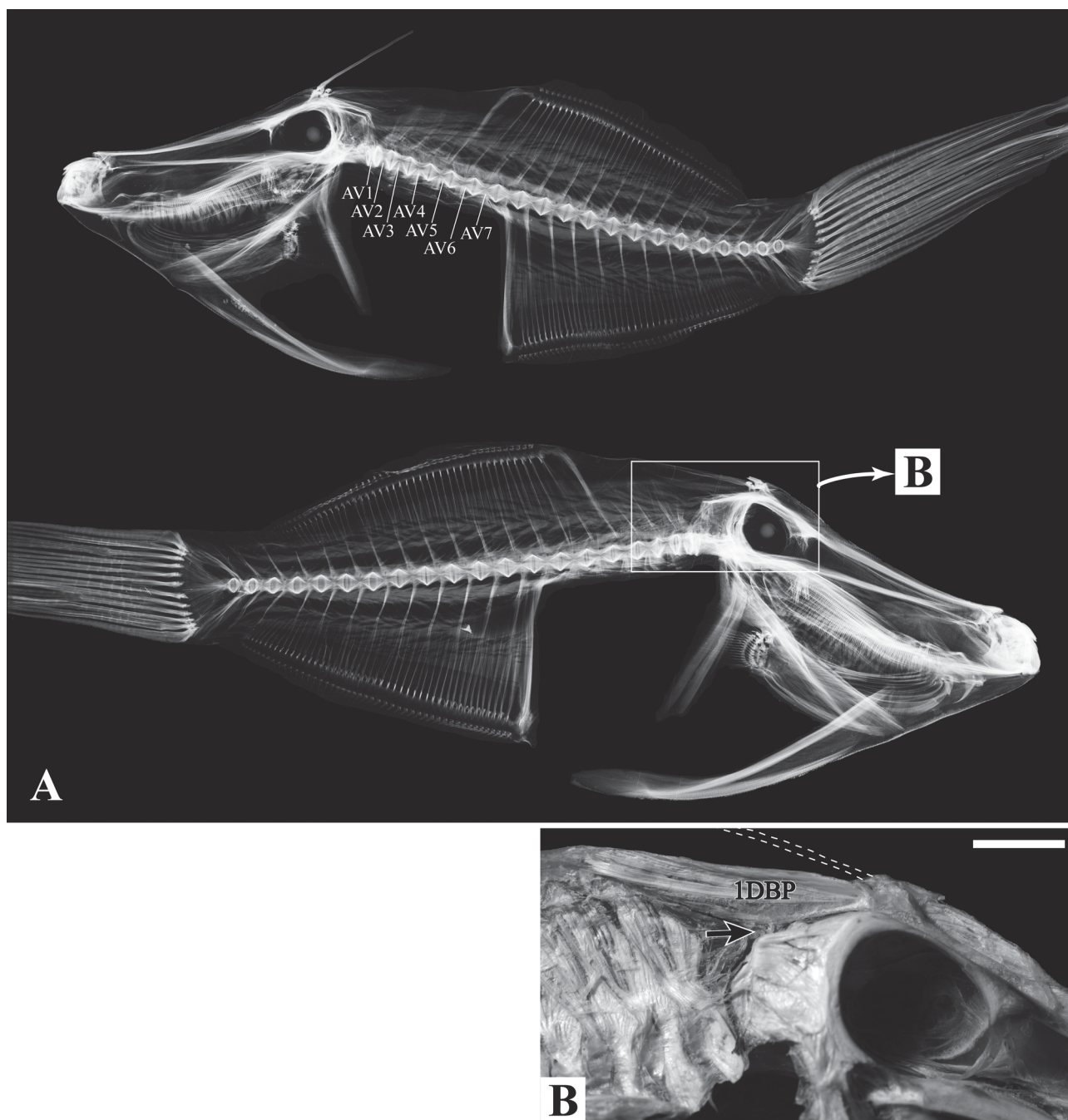


FIGURE 8. Soft radiograph (A) and enlarged photograph (B) of dried specimens of *Aluterus scriptus*. **A**, soft radiograph of KUGRF 121201 (upper, standard length = 202.8 mm) and 121202 (lower, standard length = 230.3 mm). Square shows the area enlarged in B. **B**, Enlarged photograph of the occipital region of KUGRF 121202. This specimen lacks first dorsal spine (shown by broken lines). Black arrow shows the space between ventral margin of the basal pterygiophore of the spiny dorsal fin (1DBP) and the skull. Abbreviation as in Figure 3. Scale bar = 10 mm.

Comparisons and discussion

The new fossil filefish described herein is assigned to the genus *Aluterus* by having the following characters: 21 total vertebrae (7AV + 14CV); a very slender and long first dorsal spine with tiny barbs; a single basal pterygiophore supporting the first and second dorsal spines, with the pterygiophore separated from the skull; and tiny, fine scales with slender, straight spinules.

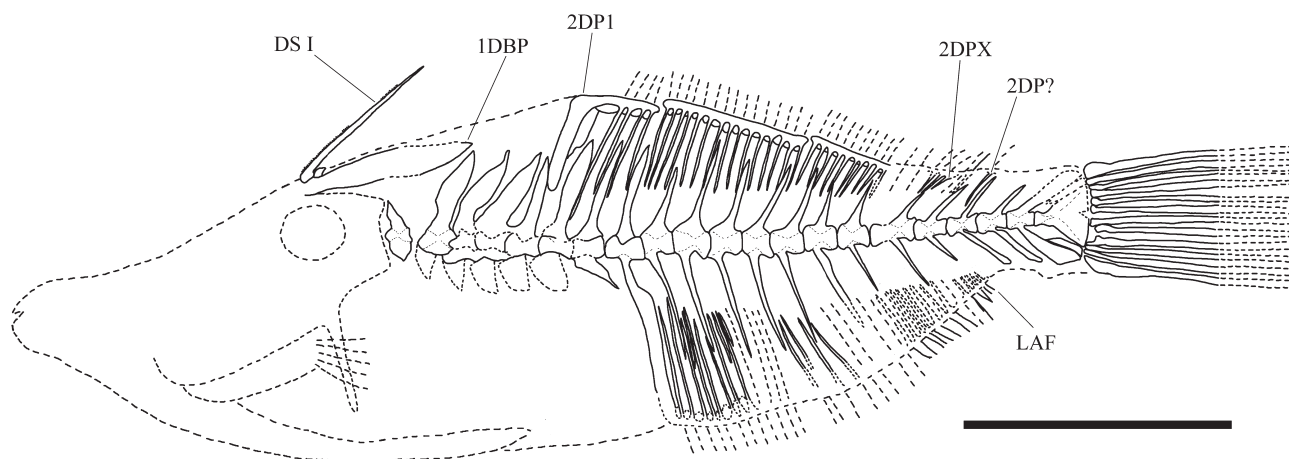


FIGURE 9. Reconstruction of *Aluterus shigensis* sp. nov. based on the part and the counterpart of the holotype. Abbreviations as in Figures 3 and 4. Scale bar = 50 mm.

In the Monacanthidae, the number of vertebrae varies among genera. Most genera, including *Aluterus*, have 7 abdominal vertebrae, and the most frequent number of caudal vertebrae among genera is 12 or 13 (Matsuura, 1979; Tyler, 1980). But species belonging to *Aluterus* have 20 (7AV + 13 CV), 21 (7AV + 14CV) or 23 (7AV + 16CV) total vertebrae. The number of total vertebrae of the new fossil species, 21(7AV + 14CV), is consistent with that of *Aluterus*. The fossil genus *Frigocanthus*, which was described by Sorbini and Tyler (2004) from the Pliocene and Pleistocene of Italy and the Pliocene of Greece, also has 21 (7AV + 14CV) total vertebrae. But *Frigocanthus* is characterized by the remarkable enlargement of scales with increasing standard length, which is a unique feature among monacanthids, and *Frigocanthus* further differs from the new fossil species of *Aluterus* by having a stout first dorsal spine with large, prominent barbs developed anterolaterally and posterolaterally (Sorbini and Tyler, 2004) unlike the very slender first dorsal spine with tiny barbs only anteriorly in the new fossil. Therefore, it is certain that the new fossil described herein does not belong to the fossil genus *Frigocanthus*.

Among the other monacanthid genera, the first dorsal spine of the genera *Eubalichthys* and *Aluterus*, especially the latter, is relatively slender and less robust and has only small to moderate barbs (Sorbini and Tyler, 2004). The very slender first dorsal spine with tiny barbs of the fossil is consistent with that of *Aluterus*.

According to Tyler (1980), the basal pterygiophore of the spiny dorsal fin of *Aluterus* is slightly smaller than in most other monacanthid fishes, and it is not broadly held ventrally to the supraoccipital and epiotics (Figure 8B). Because there is an empty space below the basal pterygiophore of the spiny dorsal fin of the fossil (Figures 3 and 5A), it seems not to be broadly held ventrally to the skull.

The tiny, fine scales with slender, straight spinules of the new fossil species of *Aluterus* (often referred to below simply as “the fossil”) have a very close resemblance to those of extant *Aluterus* species (Figure 7).

Compared to the four extant species belonging to the genus *Aluterus*, namely *A. heudelotii*, *A. monoceros*, *A. scriptus* and *A. schoepfii*, the fossil has its closest resemblance to *Aluterus scriptus* (Osbeck, 1765) by having the following characters: 21 total vertebrae (7AV + 14CV); a thin, lancet shaped basal pterygiophore of the spiny dorsal fin; a moderately slender first pterygiophore of the soft dorsal fin. Comparisons of these characters between the new fossil species, the extant *Aluterus* species, and the fossil *Frigocanthus* species are shown in Table 3.

According to Matsuura (1979), among the four extant species belonging to *Aluterus*, only *A. scriptus* has 21 total vertebrae (7AV + 14CV). The number of total vertebrae of *A. monoceros* and *A. schoepfii* is 23 (7 AV + 16CV), and that of *A. heudelotii* is 20 (7AV + 13 CV). Tyler (1980) gives the same modal values for the vertebrae of these species, but also documents that minority conditions of the number of total vertebrae exist: 22 in one out of 12 specimens of *A. schoepfii*, and 23 in one out of four specimens of *A. scriptus*.

The basal pterygiophore of the spiny dorsal fin of the fossil has a very close resemblance to that of *Aluterus scriptus* in shape (Figures 3, 5A and 8B) and size (Table 1), although the former has a slightly shallower depth than the latter. *Aluterus monoceros* and *A. schoepfii* have deeper and more robust basal pterygiophores of the spiny dorsal fin. Although *A. heudelotii* also has a lancet-shaped basal pterygiophore of the spiny dorsal fin, this species

has a relatively thick and short first dorsal spine with relatively large barbs, based on the description of Berry and Voegelé (1961) and observations of the extant specimens of this species, and a different number of total vertebrae than in the fossil.

The moderately slender first basal pterygiophore of the soft dorsal fin of the fossil resembles that of *Aluterus scriptus* in shape (Figures 3, 4, 6A and 8A). *Aluterus monoceros* and *A. schoepfii* have thick, robust first pterygiophores of the soft dorsal fin, which are crescent-shaped. Although *A. heudelotii* also has a relatively slender first pterygiophore of the soft dorsal fin compared to those of *A. monoceros* and *A. schoepfii*, in *A. heudelotii* the first dorsal spine and the number of vertebrae differ from those of the fossil. Moreover, while *A. scriptus*, *A. schoepfii*, and *A. heudelotii* and the new fossil species have five abdominal vertebrae anterior to the first pterygiophore of the soft dorsal fin, *A. monoceros* has only four abdominal vertebrae anterior to this bone.

In addition, the scales of the fossil have a very close resemblance to those of *Aluterus scriptus* in shape and size (Figure 7).

Based on the above features, the new fossil filefish described herein has its closest resemblance to the extant *Aluterus scriptus* (Osbeck, 1765). But the fossil differs from *A. scriptus* in the following ways: tiny anterior barbs are present on the first dorsal spine; the proximal tip of the first basal pterygiophore of the soft dorsal fin is located above the middle length of the neural spine of the fifth abdominal vertebra; there are fewer basal pterygiophores of the soft dorsal fin between the neural spines of the fifth abdominal to the eighth caudal vertebrae; the soft dorsal-fin base is longer than the anal-fin base; basal pterygiophores of the anal fin are absent between the haemal spines of the tenth and eleventh caudal vertebrae; and the caudal peduncle is less deep, and almost square.

The first dorsal spine of the fossil is characterized by the presence of tiny barbs in an orderly linear series on its anterior margin, while its posterior margin is smooth (Figure 5A, B). These barbs are different from scales because they are outgrowths from the first dorsal spine itself (Figure 5B) and are preserved in an orderly manner even though tiny scales are preserved randomly over almost the entire body. By contrast, the first dorsal spine of *Aluterus scriptus* is entirely covered with tiny spinule-like scales and there are no barbs developed in an orderly manner on its anterior margin like those of the fossil (Figure 5C). These features of the first dorsal spine of the fossil also distinguish it from all of the extant *Aluterus* species (Table 3). According to Sorbini and Tyler (2004), in monacanthid fishes the first dorsal spine become more slender and less stout with barbs reducing or lacking in derived genera, including *Aluterus*.

Although the shape of the first basal pterygiophore of the soft dorsal fin of the fossil has a resemblance to that of *Aluterus scriptus*, as mentioned above, its proximal tip is located higher than in the latter. In *A. scriptus*, the proximal tip of the first pterygiophore of the soft dorsal fin is located at about the middle length of the neural spine of the fifth abdominal vertebra (Figure 8A). But in the fossil, the proximal tip of this pterygiophore does not reach as far ventrally as does that of *A. scriptus* and it is located above the middle length of the neural spine of the fifth abdominal vertebra (Figures 3, 4 and 6A).

The numbers of pterygiophores of the soft dorsal fin between two adjacent neural spines from that of the fifth abdominal to that of the thirteenth caudal vertebrae are shown in Table 2 with reference to the fossil and five specimens of *Aluterus scriptus*. The numbers for these six specimens show different patterns. Although this could be an individual variation, at least the number of pterygiophores of the soft dorsal fin between the neural spines of the fifth abdominal and the eighth caudal vertebrae of the fossil (the pterygiophores posterior to the eighth caudal vertebra are incompletely preserved) is 29 and is less than those of the five specimens of *A. scriptus*, 32–37. But the total number of the pterygiophores of the soft dorsal fin of the fossil is unknown.

In the fossil, the soft dorsal-fin base is longer than the anal-fin base (Table 1). But in the extant species of *Aluterus*, including *A. scriptus*, the soft dorsal-fin base is shorter than the anal-fin base (Table 3), except for the minority condition of large specimens of *A. monoceros* over 500 mm SL having the soft dorsal-fin base equal to or slightly longer than the anal-fin base (Sorbini and Tyler, 2004). Sorbini and Tyler (2004) considered the soft dorsal-fin base being longer than the anal-fin base as an ancestral character for monacanthids.

In the fossil, pterygiophores of the anal fin are absent between the haemal spines of the tenth and eleventh caudal vertebrae (Figures 3, 4 and 6B). Unlike the fossil, pterygiophores of the anal fin of *Aluterus scriptus* are present between the haemal spines of the tenth and eleventh caudal vertebrae (Figure 8A). This indicates that the fossil has a shorter anal fin anteroposteriorly than that of *A. scriptus*. However, this difference may be because of poor preservation of the fossil.

The caudal peduncle depth (CD: the least depth of the caudal peduncle) of the fossil is estimated to be 23.3

mm. Its ratio to the length l (CD/l) is 0.19, which is less than those of specimens of *Aluterus scriptus* (Table 1). This indicates that the fossil has a relatively shallower caudal peduncle than that of *A. scriptus*. Moreover, the caudal peduncle length (CL) of the fossil is greater, and the ratio of the caudal peduncle depth to caudal peduncle length (CD/CL) of the fossil is 1.23 and less than those of specimens of *A. scriptus* (Table 1). These measurements suggest that the fossil has a nearly square caudal peduncle, whereas *A. scriptus* has a deeper than long caudal peduncle (Berry and Voegelé, 1961). This feature of the fossil also distinguishes it from the other extant *Aluterus* species except for *A. heudelotii* (Table 3).

Based on the above, although the fossil described herein is probably closely related to the extant *Aluterus scriptus* (Osbeck, 1765), the fossil has a distinctive set of characters that separates it from both *A. scriptus* and the other three extant *Aluterus* species (Table 3). Thus, this fossil is a new species having a close resemblance to the extant species of *Aluterus*, even though the fossil lacks some significant features utilized to identify extant species of this genus, such as those of the pelvic girdle and complete sets of the soft dorsal- and anal-fin rays (Matsuura, 1979; Tyler, 1980).

Among monacanthids, the species of *Aluterus* tend to grow relatively large: most species obtain over 500 mm SL, especially *A. scriptus*, which reaches up to 800 mm SL, whereas *A. heudelotii* only grows up to 300 mm SL (Berry and Voegelé, 1961; Matsuura, 2002). Considering this, the holotype of *Aluterus shigensis* **sp. nov.** described herein, whose standard length is estimated to be about 200 mm (Table 1), could be a juvenile or young adult individual.

The extant species of *Aluterus* are usually distributed in tropical and temperate waters (Matsuura, 2002). Among them, *A. monoceros* and *A. scriptus* are distributed worldwide, including the Northwest Pacific (e.g., Nakabo, 2000; Matsuura, 2002). The distribution of *A. scriptus* ranges from 46°N to 38°S (Izzo *et al.*, 2010) in lagoons and reefs of tropical and subtropical waters (Matsuura, 2002). Recently, it is reported that this species is passively introduced into temperate waters by the warm Kuroshio Current in Japan (e.g., Shimizu *et al.*, 2009). Similarly, in Argentina it is reported that this species can also live in temperate waters where warm currents flow (Izzo *et al.*, 2010).

In the Middle Miocene Bessho Formation, the influence of warm currents is suggested by the fossil occurrence of *Mizuhobaris izumoensis* (Kosaka and Taguchi, 1983) and a planktonic foraminiferal fossil assemblage (Kato *et al.*, 2011). The occurrence of *Aluterus shigensis* **sp. nov.**, which has a close resemblance to *Aluterus scriptus*, from the Bessho Formation is consistent with those suggestions.

The extant species of *Aluterus* live in shallow coastal waters down to 150 m (Matsuura, 2002; Luiz Jr *et al.*, 2008). On the other hand, the sedimentary environment of the Bessho Formation is estimated to be upper to upper middle bathyal by the benthic foraminiferal fossil assemblage (Kato *et al.*, 2011) and continental slope by the molluscan and benthic foraminiferal fossil assemblages (Tanaka, 1959; Masatani and Ichimura, 1970; Nobuhara and Ohtori, 2009). With regard to fossil fishes, deep-water taxa such as myctophids and macrourids occur as well as coastal fishes such as clupeids from the Bessho Formation. Considering that the skeleton of *Aluterus shigensis* **sp. nov.** is mostly articulated, it is suggested that this fossil filefish died and sank to its depositional place nearly intact without much disarticulation, and decayed slowly, as is the case with other fossil fishes occurring in the Bessho Formation (Ohe and Koike, 1998). The disarticulation and displacement of soft fin rays of the soft dorsal and anal fins may suggest the influence of bottom currents (Elder and Smith, 1984).

Fossil filefishes are known from the Middle to Upper Pliocene and the Lower Pleistocene, 3.1–1.3 Ma (Sorbini and Tyler, 2004) of northeast (Sorbini, 1988; Landini and Sorbini, 1992; Landini and Sorbini, 1993) and southeast Italy (Landini and Menesini, 1978). These numerous fossils are mostly well preserved fully articulated skeletons with skulls, and have been reviewed, with the description of two new species of a new genus, *Frigocanthus stroppanobili* and *F. margaritatus*, by Sorbini and Tyler (2004). According to Sorbini and Tyler (2004), *Frigocanthus* is characterized mainly by the enlargement of scales with increasing body size: in *F. margaritatus*, individual scales are up to 7.2 mm in the largest specimen (310 mm SL), whereas in *F. stroppanobili* scales are aggregated into large composite scale plates. They performed a phylogenetic analysis based on nine morphological features and showed that *Frigocanthus* is most closely related to *Aluterus*, sharing such characters as a simplified pelvic girdle, six branchiostegal rays, and an increased number of vertebrae. But *Frigocanthus* differs from *Aluterus* by having the following characters: the enlargement of scales; the soft dorsal-fin base longer than the anal-fin base, and the stout first dorsal spine with well-developed barbs (Table 3).

TABLE 3. The comparisons of several osteological characters among *Aluterus shigenis* sp. nov., *Aluterus* species and *Frigocanthus* species. Some characters are based on descriptions and illustrations of Berry and Voegelé (1961) and Sorbini and Tyler (2004). Because the measurements and descriptions of the caudal peduncle of *Frigocanthus* spp. are not available, the caudal peduncle is considered to be deeper than long based on the figures in Sorbini and Tyler (2004), adding “?” at the end.

species	First dorsal spine	Basal pterygiophore of the spiny dorsal fin	Number of total vertebrae	Caudal peduncle	First pterygiophore of the soft dorsal fin	Length of soft dorsal-fin base and anal-fin base	Enlarged scales
<i>Aluterus shigenis</i> sp. nov.	spine slender and long, tiny barbs developed only on its anterior margin	thin, lancet-like shaped	21 (7AV + 14CV)	nearly equal depth and length	slender	dorsal-fin base longer	absent
<i>Aluterus scriptus</i>	spine slender and long, entirely covered with tiny spinule-like scales	thin, lancet-like shaped	21 (7AV + 14CV)	deeper than long nearly equal	slender	anal-fin base longer	absent
<i>Aluterus heudelotii</i>	spine relatively thick and short, relatively large barbs developed anteroposteriorly	thin, lancet-like shaped	20 (7AV + 13CV)	depth and length	slender	anal-fin base longer	absent
<i>Aluterus monoceros</i>	spine slender and long, entirely smooth	deep and robust	23 (7AV + 16CV)	longer than deep	thick, robust and crescent-shaped	anal-fin base longer	absent
<i>Aluterus schoepfii</i>	spine slender and long, tiny barbs developed posteriorly	deep and robust	23 (7AV + 16CV)	deeper than long	thick, robust and crescent-shaped	anal-fin base longer	absent
<i>Frigocanthus</i> spp.	spine stout and long, prominent barbs developed anteroposteriorly	thin, lancet-like shaped	21 (7AV + 14CV)	deeper than long?	slender	dorsal-fin base longer	present

In addition to the numerous complete fossils of *Frigocanthus stroppanobili* and *F. margaritatus* from localities in Italy, both of these species are known from the Upper Pliocene (3.1–2.5 Ma) of Crete, Greece, although only from fragmentary remains (Gaudant, 2001; Sorbini and Tyler, 2004).

Fossils described as *Aluterus* sp., based only on vertebrae, are also known from the Middle Miocene (Langhian) and Lower Pliocene in North Carolina (Purdy *et al.*, 2001). It is pointed out that these fossil vertebrae have a resemblance to those of extant *Aluterus schoepfii* (Purdy *et al.*, 2001). This fossil record from the Middle Miocene in North Carolina is of about the same age as or older than the Bessho Formation.

Both Matsuura (1979) and Tyler (1980) pointed out that *Aluterus* is a relatively derived genus among the Monacanthidae based on osteological characters such as the decreased size and closeness of association of the basal pterygiophore of the spiny dorsal fin with the skull, increased number of vertebrae, and relatively simplified (without dorsal lobe and incising scales) pelvic girdle. In addition, according to Sorbini and Tyler (2004), the slender first dorsal spine with small to moderate barbs and the soft dorsal-fin base being shorter than the anal-fin base are also derived characters of *Aluterus*. The fossil occurrences of *Aluterus* from the Middle Miocene and of *Frigocanthus*, which is closely related to *Aluterus* (Sorbini and Tyler, 2004), from the Pliocene and Pleistocene indicate that the derivation of the *Aluterus* + *Frigocanthus* clade of the family Monacanthidae was already relatively advanced by the Middle Miocene.

The fossil occurrence of filefish from the Bessho Formation in Nagano Prefecture, central Japan indicates that monacanthid fishes, especially the species belonging to the genus *Aluterus*, had already been derived and were distributed at least in the Northwest Atlantic and Northwest Pacific in the Middle Miocene. In addition, the close resemblance of the extant species of *Aluterus* to the Middle Miocene species *Aluterus shigensis* **sp. nov.** indicates that, about 13 Ma in the Middle Miocene, the species of this clade already had obtained the highly derived features that characterize the Recent species of this genus.

Acknowledgements

We would like to express our deepest gratitude to Carole Baldwin, Jeff Williams and Sandra Raredon (National Museum of Natural History, Smithsonian Institution, USA) for their very kind help in sending radiographs of extant specimens of *Aluterus*. We sincerely thank Yoshiaki Kai (Maizuru Fisheries Research Station, Kyoto University, Japan) for his kindness in permitting access to the extant fish specimens at the research station. We are also very grateful to Katsutoshi Watanabe and Tsutomu Hikida (Kyoto University, Japan) for their kind help in taking radiographs of dried extant specimens, and Rie Fujii (Kyoto University, Japan) for her help in SEM usage. Fumito Yokouchi (Matsumoto City Shiga Fossil Museum, Japan) is thanked for agreeing to deposit the new fossil filefish in the Museum. We also thank Kazumi Zenitani and Ayako Ohtsuki (Kyoto University, Japan) for their help in obtaining literature. We further wish to express our sincere appreciation to James C. Tyler (National Museum of Natural History, Smithsonian Institution, USA) and Gloria Arratia (Natural History Museum and Biodiversity Institute, University of Kansas, USA) for their careful and critical reviews of the manuscript and valuable comments that improved this paper.

References

- Berg, L.S. (1940) Classification of fishes both Recent and fossil. *Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS*, 5 (2), 87–345. [in Russian; original title translated]
- Berry, F.H. & Voegelé, L.E. (1961) Filefishes (Monacanthidae) of the Western North Atlantic. *Fishery Bulletin of the Fish and Wildlife Service*, 61, 57–109.
- Blow, W.H. (1969) Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. In: Brönnimann, P. & Renz, H.H. (Eds.), *Proceedings of the First International Conference on Planktonic Microfossils. Vol. 1. Geneva. 1967*. E.J. Brill, Leiden, Netherlands, pp. 199–421.
- Cloquet, H. (1816) *Dictionnaire des Sciences Naturelles. Vol. 1*. F.G. Levrault, Strasbourg, 698 pp. [in French]
- Elder, R.L. & Smith, G.R. (1984) Fish taphonomy and paleoecology. *Géobios, Mémoire Spécial*, 8, 287–291.
- Gaudant, P.J. (2001) Amnissos: un gisement clé pour la connaissance de l'ichthyofaune du Pliocène supérieur de Crète. *Annalen des Naturhistorischen Museums in Wien*, 102A, 131–187. [in French with English abstract]
- Harayama, S. (2006) The Northern Fossa Magna—the Hida Mountains. Split of the Asian Continent and tectonics of island arc.

- Outline. In: The Geological Society of Japan (Ed.), *The Chubu Region*. Asakura Publishing Co., Tokyo, pp. 316–317. [in Japanese; original title translated]
- Hirota, K. & Barnes, L.G. (1995) A new species of Middle Miocene sperm whale of the genus *Scaldicetus* (Cetacea; Physteridae) from Shiga-mura, Japan. *Island Arc*, 3, 453–472.
<http://dx.doi.org/10.1111/j.1440-1738.1994.tb00125.x>
- Honma, F. (1927) The geological structures of central Nagano (outline). *Journal of the Geological Society of Japan*, 34 (403), 132–153. [in Japanese; original title translated]
- Hutchins, J.B. (1977) Descriptions of three new genera and eight new species of monacanthid fishes from Australia. *Records of the Western Australian Museum*, 5 (1), 3–58.
- Izzo, P., Milessi, A.C., Ortega, L. & Segura, A.M. (2010) First record of *Aluterus scriptus* (Monacanthidae) in Mar del Plata, Argentina. *Marine Biodiversity Records*, 3, 1–2.
<http://dx.doi.org/10.1017/s1755267210000369>
- Kano, K., Kato, H., Yanagisawa, Y. & Yoshida, F. (1991) Stratigraphy and Geologic History of the Cenozoic of Japan. *Report, Geological Survey of Japan*, 274, 1–114. [in Japanese with English abstract]
- Kato, S., Hiramatsu, C., Miwa, M. & Nobuhara, T. (2011) Geological age and sedimentary environment of the Anazawa Limestone in the Middle Miocene Bessho Formation, Nagano Prefecture, central Japan. *Bulletin of the Mizunami Fossil Museum*, 37, 135–147. [in Japanese with English abstract]
- Kobayashi, Y. (2006) The Northern Fossa Magna—the Hida Mountains. Split of the Asian Continent and tectonics of island arc. Black mudstones (shales) of the Bessho Formation. Deepsea sediments formed by the opening of the Japan Sea. In: Geological Society of Japan (Ed.), *The Chubu Region*. Asakura Publishing Co., Tokyo, pp. 318–319. [in Japanese; original title translated]
- Kosaka, T. & Taguchi, Y. (1983) Discovery of fossil Argonautinae from the Bessho Formation of Northern Fossa Magna, Japan and its geohistorical significance. *Earth Science (Chikyu-Kagaku)*, 4, 187–193. [in Japanese with English abstract]
- Kosaka, T., Midori, T., Hoya-nagi, K., Kubota, M. & Miyahigashi, Y. (1992) Late Cenozoic stratigraphy and paleogeographic changes in the Northern Fossa Magna. *Memoirs of the Geological Society of Japan*, 37, 71–83. [in Japanese with English abstract]
- Kosaka, T., Nakayama, C., Koshimizu, S., Shiba, M., Bizen, N. & Isomura, T. (1998) The geological age of the middle Miocene formations in the Northern Fossa Magna region, central Japan —The foraminiferal and fission-track ages of the Uchimura and Bessho Formations—. *Earth Science (Chikyu Kagaku)*, 52, 502–507.
- Landini, W. & Menesini, E. (1978) L'ittiofauna plio-pleistocenica della sezione della Vrica (Crotone-Calabria) [The Plio-Pleistocene ichthyofauna of the Vrica section (Calabria, Italy)]. *Bollettino della Società Paleontologica Italiana*, 17 (2), 143–175. [in Italian with English abstract]
- Landini, W. & Sorbini, L. (1992) The teleost fishes of the Miocene and Pliocene of Italy: New data. *Geobios*, 25 (supplement), 151–157. [in French with English abstract and figure captions; original title translated]
- Landini, W. & Sorbini, L. (1993) Biogeographic and palaeoclimatic relationships of the Middle Pliocene ichthyofauna of the Samoggia Torrent (Bologna, Italy). *Ciências da Terra (UNL), Proceedings of the 1st Regional Committee on Atlantic Neogene Stratigraphy (R.C.A.N.S) Congress, Lisboa*, 12, 83–89.
- Luiz Jr., O.J., Carvalho-Filho, A., Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L. & Sazima, I. (2008) The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa*, 1807, 1–25.
- Masatani, K. & Ichimura, T. (1970) Petroleum geology of the northern part of the Fossa Magna. *Journal of the Japanese association of petroleum technologists*, 35 (1), 1–12. [in Japanese with English abstract]
- Matsuura, K. (1979) Phylogeny of the superfamily Balistoidea (Pisces: Tetraodontiformes). *Memoirs of the Faculty of Fisheries Hokkaido University*, 26, 49–169.
- Matsuura, K. (2002) Monacanthidae. In: Carpenter, K.E. (Ed.), *The living Marine Resources of the Western Central Atlantic. FAO Species Identification Guide for Fishery Purposes. Vol. 3. Bony Fishes Part 2 (Opistognathidae to Molidae). Sea Turtles and Marine Mammals*. FAO, Rome, pp. 1970–1979.
- Nakabo, T. (2000) *Fishes of Japan with Pictorial Keys to the Species. 2nd edition*. Tokai University Press, Tokyo, 1749 pp. [in Japanese]
- Nardo, G. (1842) Considerazioni sopra alcune nuove famiglie de' syngnathi e dei plectognathi, e sui caratteri anatomiche le distinguono. *Atti della Quarta Riunione degli Scienziati Italiani (tenuta in Padova)*, 244–245. [in Italian]
- Nelson, J.S. (2006) *Fishes of the World. 4th Edition*. John Wiley & Sons, New Jersey, 601 pp.
- Nobuhara, T. & Ohtori, Y. (2009) Lithological description of boring core samples of the lower Middle Miocene methane-seep carbonate mound (the Anazawa Limestone) in the Bessho Formation, Nagano Prefecture, central Japan. *Geoscience Reports of Shizuoka University*, 36, 9–26. [in Japanese with English abstract]
- Ohe, F. & Koike, H. (1998) Fish assemblage of the Miocene Bessho Formation, Toyoshina-machi, Minamiazumi-gun, Nagano Prefecture. *Research Report of the Shinshu-shinmachi Fossil Museum*, 1, 33–39. [in Japanese with English abstract]
- Osbeck, P. (1765) *Reise nach Ostindien und China. Aus dem Schwedischen übersetzt von J.G. Georgi*. J.C. Koppe, Rostock, 637 pp. [in German]
- Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L. & Slaughter, B.H. (2001) Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In: Ray, C.E. & Bohaska, D.J. (Eds.), *Geology and*

- Paleontology of the Lee Creek Mine, North Carolina, 3. Smithsonian Contributions to Paleobiology. Vol. 90.* Smithsonian Institution Press, Washington, D.C., pp. 71–202.
- Schultze, H.-P. & Arratia, G. (2013) The caudal skeleton of basal teleosts, its conventions, and some of its major evolutionary novelties in a temporal dimension. *In: Arratia, G., Schultze, H.-P. & Wilson, M.V.H. (Eds.), Mesozoic Fishes 5-Global Diversity and Evolution.* Verlag Dr. Friedrich Pfeil, München, pp. 187–246.
- Seki, J. (1983) Geological map of Akashina region, 1: 25,000. *In: Editorial Committee of The History of Akashina Town (Ed.), The History of Akashina Town. Vol. 1.* The Board of Education of Akashina Town, Subcommittee on the Publication of The History of Akashina Town, Nagano, pp. 1216. [in Japanese; original title translated]
- Shimizu, N., Kawata, K., Matsuura, Y., Shigeta, T., Sakai, Y., Hashimoto, H. & Ohtsuka, S. (2009) Record of the scrawled filefish *Aluterus scriptus* (Family: Monacanthidae), a tropical/warm-temperate fish found off Osaki-Kamijima Island, Seto Inland Sea, Japan. *Bulletin of the Hiroshima University Museum*, 1, 85–89. [in Japanese with English abstract]
- Sorbini, C. & Tyler, J.C. (2004) Review of the fossil file fishes of the family Monacanthidae (Tetraodontiformes), Pliocene and Pleistocene of Europe, with a new genus, *Frigocanthus*, and two new species related to the Recent *Aluterus*. *Bollettino del Museo Civico di Storia Naturale di Verona*, 28, 41–76. [Geologia Paleontologia Preistoria]
- Sorbini, L. (1988) Biogeography and climatology of Pliocene and Messinian fossil fish of eastern-central Italy. *Bollettino del Museo Civico di Storia Naturale di Verona*, 14, 1–85.
- Tanaka, K. & Seki, J. (1966) The Neogene Tertiary of northern area of Matsumoto City, central Japan. *Bulletin of the Faculty of Education Shinshu University*, 18, 139–163. [in Japanese; original title translated]
- Tanaka, K. (1959) Molluscan fossils from central Shinano, Nagano Prefecture, Japan (part 1) —Fossils from Akanuda Limestone—. *Journal of the Shinshu University Faculty of Education*, 8, 115–133.
- Tyler, J.C. (1980) Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). *NOAA Technical Report NMFS Circ.*, 434, 1–422.